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I am submitting herewith a dissertation written by Ali Abdul Ghani Al-Talib, entitled "Maternal Effects in Angus Bull and Heifer Calves Fed at Different Post-Weaning Nutritional Levels." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Animal Science.

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A

MATERNAL EFFECTS IN ANGUS BULL AND HEIFER CALVES FED AT DIFFERENT POST-WEANING NUTRITIONAL LEVELS

A Dissertation

Presented for the

Doctor of Philosophy

Degree

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ABSTRACT

Data were obtained at weaning from 1521 Angus calves sired by 145 bulls during a period of ten years (1969 to 1978). Yearling data were obtained from 1388 Angus calves sired by 135 bulls during a period of nine years (1970 to 1978). The calves supplying these data were raised at the University of Tennessee Plateau Experiment Station, Crossville, Tennessee. The traits recorded on each animal at weaning (average age, 230 days) and at post-weaning (average age, 385 days) were Average Daily Gain, Body Weight, Body Length, Hip Height, Hip Width, Fat Thickness, Hide Thickness, Heart Girth, Condition Score and Type Score.

Post-weaning feeding was on a relatively high forage, low concentration ration. Heifers were fed at a restricted level, as compared to bulls to produce an average daily gain of approximately one pound per day, with limited fat production.

All records were adjusted by using constants obtained by least-squares procedures to remove variation due to differences in age of calf, sex of calf and age of dam. Nested within-year analyses were performed. One model was used to obtain estimates of components of variance due to sire differences, and another model was used to obtain estimates of components of variance due to dam differences. Analyses by the second model were performed after adjusting the data to remove variation due to sire and year differences. The estimate of the component of variance due to differences in maternal influence was calculated as

the difference between the estimate of the component of variance due to total variation between dams and the estimate of the component of variance due to sire differences.

Results showed maternal influence on average daily gain (ADG) to weaning in bulls to be greater than that on ADG of heifers. Sire differences in all but two traits, average daily gain and hide thickness, were significant ($P<0.01$) at post-weaning, but at weaning, sire differences were significant ($P<0.01$) in only four traits: average daily gain, heart girth, condition score and type score. Differences between sires were responsible for a significant portion of the variance in body weight of both bull ($P<0.01$) and heifer calves ($P<0.01$), and bull calves were significantly ($P<0.01$) heavier than heifer calves. The male data were responsible for the increases in maternal variance percentages from weaning to post-weaning with respect to all but two traits in males, average daily gain and fat thickness which showed the expected decrease. These two traits are obviously directly affected by nutrient supply. The differences between males and females with respect to changes in relative importance of maternal influence from weaning to post-weaning indicate that females, during the post-weaning period, tend to reflect differences in their individual potential for growth more than do males which, apparently, reflect persisting maternal effects during the post-weaning period. In general, maternal variance percentages are greater in females at weaning and greater in males at post-weaning. Maternal variance is of considerable magnitude in several traits both at weaning and post-weaning. However, specific recommendations as to adjustments to remove maternal variance are not justified at this time.

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CHAPTER I

INTRODUCTION

The beef cattle industry in the Southeast and other grassland areas is primarily a cow-and-calf program. The importance of maternal effects on the growth of young mammals has been recognized since the earliest attempts to improve livestock production, and maternal effects in animals have been studied extensively both because of their theoretical interest and because of their economic importance in domestic mammals. Many studies have suggested a negative genetic correlation between gene transmitted and maternal environmental effects. The study of maternal influence is complicated because a dam transmits a sample half of her genes to her young, and her genotype is also expressed in the prenatal and postnatal circumstances which influence the young. All factors which affect the growth of the young animal are of great economic importance in animal production. Many of these factors do not affect the development of a young animal directly, but rather through its maternal environment.

In the present study both maternal effects and sire effects as genetic factors and nutritional effects as environmental factors were considered. The purpose was to estimate maternal effects in both sexes of offspring combined together and maternal effects in bull and heifer offspring separately. Traits studied at weaning (at about seven months of age) and at post-weaning (at about one year of age)

were: body weight, average daily gain, hip height, hip width, hearth girth, hide thickness, fat thickness, body length, type score and condition score.

CHAPTER II

REVIEW OF LITERATURE

I. NUTRITIONAL EFFECTS

The feed requirement of the brood cow herd is probably the largest single item of expense in a commercial cow-calf operation. The cost of producing a feeder calf has been estimated to be as large as 50 percent of total costs in a cow-calf enterprise. The level of feeding is very important in beef cattle. Most producers trust that a comparatively low level of feeding during the second year of life increases rumen development. In comparisons of prices of feeder cattle, when fed to a constant age, with prices of slaughter cattle, it has been found that, in all cases, there appears to be a closer relationship between prices of feeder cattle and the approximate slaughter grade for which they might qualify than between prices of the corresponding feeder and slaughter grades.

In a study of the growth of lambs before and after parturition in relation to the plane of nutrition of the ewe, Wallace (1948) indicated a large effect of maternal nutrition, from day 48 of pregnancy to term, on birth weight of both single and twin lambs, and the effect was greater in twins, those from low-plane ewes weighing only 50 to 60 percent as much as those from high-plane ewes.

Notter et al. (1978a) reported that the wide range of cattle types presently available to the beef producer allows considerable flexibility in matching specific germ plasm resources to specific climatic, nutritional and management environments in order to maximize the efficiency of beef production. In a study of feed consumption, daily gain and feed required per unit of gain in beef calves, Bogart and England (1971) reported that bulls eat no more per unit of body weight than do heifers, but they make greater daily gains. Hence, bulls require much less feed to make a unit of gain than do heifers. They added that much of the variation in daily gain per unit of gain is accounted for by variation in daily feed consumed and feed required. Also, much of the variation in feed required is accounted for by variation in daily gain and daily feed consumed per unit of gain.

Fifty-eight yearling Hereford heifers were individually fed on different levels of nutrition (127 and 196 k cal of digestible energy/kg Bw/day). Following calving they were then fed 1.4 kg of corn and alfalfa hay ad libitum, by Christenson et al. (1967). Results showed that heifers fed the high energy ration produced heavier calves at birth but experienced more calving difficulty than heifers fed the low energy ration and gained more weight during the last half of the gestation period.

From a study of Angus, Hereford and Polled Hereford bulls, Marlowe (1962) indicated that bull weight measured between 12 and 24 months of age accounted for 70.7, 69.2, and 76.7 percent of the variation in weaning weight of progeny of Angus, Hereford and Polled Hereford bulls, respectively. Breed of bull had no significant influence on weight. Angus

bulls were lighter than Herefords at all ages. There was no significant weight difference between Herefords and Polled Herefords at 12 to 48 months of age. However, Herefords were slightly heavier at maturity.

Totusek et al. (1959) fed two groups of 30 cows each at two different levels. The high-level ration consisted of hay fed ad libitum, 2.5 lb of cotton seed meal and free access to milo from late summer to calving. They found that cows on this ration were much fatter prior to calving than those fed at a low level (hay ad lib. and 2.5 lb of cotton seed meal). It was concluded that a high degree of body fat during the growth period appeared to affect adversely the productive ability of heifers, while a high degree of fatness induced in mature cows had little influence on their productivity.

A group of 206 Angus and Hereford females were used in four trials by Holloway and Totusek (1973) to determine the effects of three preweaning planes of nutrition attained by: (1) weaning at 140 days, (2) weaning at 240-days and (3) creep-feeding and weaning at 240-days. They reported that heart girth, body weight, body length and height at hooks and withers were significantly ($P<0.05$) affected by treatment to 1.5 years. There was no significant difference ($P>0.10$) in any measurement of height between the 240-day weaned and creep-fed groups, although a significant ($P<0.05$) difference between extreme treatments was apparent at 1.5 years of age.

Totusek (1968) compared weaning weights of calves out of heifers raised under different systems: (1) weaned at 140 days of age, (2) weaned at 240-days of age and (3) creep-fed and weaned at 240-days

of age. Heifers weaned at 140 days of age produced calves that weighed about 10 kg more than those out of creep-fed heifers. Similar results were obtained by Martin et al. (1970).

From data including 2286 calf weaning weight records, Mangus and Brinks (1971) found that higher preweaning nutritional levels and high cow inbreeding level have detrimental effects upon beef cow productivity. They found also that weaning weight is a poor predictor of subsequent cow productivity.

Gifford (1953) listed three limiting factors which probably affect milk yield in beef cows. These factors are: (1) genetic influences, (2) feeding and management and (3) the calf effects on the physiological processes of milk secretion.

Neville (1962) fed three rations: (1) grass silage and 1 lb of cotton seed meal, (2) corn silage and 1 lb of cotton seed meal and (3) corn silage, 1 lb of cotton seed meal and limited winter pasture. He found that calf growth rate due to these nutritional treatments can be affected by: (1) average milk production of the dam within each nutritional treatment which is in turn affected by inherent milk producing ability and nutrition of the dam and (2) general plane of nutrition other than milk available to the calf.

Harris et al. (1962), studying the effect of winter feeding level of beef cows upon milk production and calf performance, indicated that beef cows on limited winter feed decline materially in milk production

during the period of limited feeding but still respond to lush grazing by an increase in milk yield. However, calves from such cows are lighter at weaning than those from more liberally fed dams.

Christian et al. (1965) pointed out that weaning weight was influenced by milk production, but did not affect carcass grade significantly. They found a significant negative correlation between the weaning weight of the dam and her butterfat production to 60 days of age of her calf. The negative correlations between weaning weight and other measures of milk production were almost significant ($P<0.05$). They suggested from these results that a negative genetic or environmental correlation, or both, exists between weaning performance of the dam and the maternal environment she provides for her calf. During the post-weaning feeding period, the average daily gain (ADG) was found to increase significantly with increased weaning weight.

Studying nine body measurements which were: height at withers, height at hips, width at the point of shoulders, depth of body at fore-girth, width at pelvic bones, heart girth, width at loin, diagonal length from point of shoulder to pin bone and depth of body at rear flank region, in addition to body weight recorded on 267 Hereford and Angus bulls at 4, 8 and 12 months of age, Brown et al. (1973a) found that the complex of genes influencing size or shape tended to have similar effects at the three different ages. However, the correlations indicated that, when equal weighting was given to each of the 10 measures of size as in the first principal component in a multivariate analysis, bulls selected at one age on this single composite value could be quite different in shape

at later ages. They added that this result explained the likelihood that unrestricted selection based on a composite character such as weight, size or gain would produce animals of variable measurements or shape.

Rate of fattening and/or gain was found to be positively related to body measurements, but it was concluded that form and function in these respects are not closely enough correlated to be useful for predicting future performance (Lush, 1928, 1932). Brown et al. (1973b) reported that the amount of feed consumed by an animal is expected to be proportional to the size of the animal. Genes influencing capacity and gain have a strong influence on feed consumed; therefore, the 4-month measurements which showed the strong relationships to feed consumed showed strong relationships also to test gain. However, several measurements on Angus bulls were highly correlated with feed consumed and were not strongly related to test gain. Hip width was the only Angus measurement which did not show a moderate to large relationship to feed consumed.

II. MATERNAL EFFECTS

The improvement of beef calves in preweaning weights is primarily dependent upon increased preweaning growth protential of calves and maternal ability of cows. Maternal effects of the dam cannot be measured directly. Usually they are measured by the offspring's performance. Maternal effects should be greatest during two periods in the young mammal's life. The first period is from conception to birth. The second is from birth to weaning.

In beef cattle, the cow affects the genetic variance and heritability both by the genes she transmits and by the maternal environment she provides. Maternal environmental influence is a classic mammalian example of indirect genetic effect since the dam's maternal ability is contributed to by her own heredity.

Knowledge of the relationship between direct genetic effects and maternal effects is desirable in studying traits affected by maternal influences, as emphasized by Brown (1977). He defined maternal effect as a phenotypic value of a dam measureable only as a component part of her offspring's phenotypic value.

Hunter (1956) defined the maternal effects as the sum of the effects of those maternal factors which influence the growth of the young after fertilization of the egg, a combination of pre-natal and post-natal elements.

There are two areas of interest concerning maternal effects. The first area of interest is involved with biases in heritability estimates caused by the presence of maternal effects. The second area of interest is the genetic variation in maternal effects and the correlation between direct genetic and maternal genetic effects. Van Vleck (1977) found maternal genetic variance to be larger than direct genetic variance.

Willham (1972) explained that the phenotypic value of the maternal effects is probably much more complex than just the sum of a genic and environmental value. He added that there are permanent maternal effects of a dam as expressed in her offspring. Maternal effects were a more important source of variation in birth weight, condition score

and weaning index (with equal emphasis on type and average daily gain), than in average daily gain (ADG) or type score (Butts, 1966).

Data from Virginia beef cattle cross-breeding experiments were used to study maternal effects by Gaines et al. (1970). There were three breeds represented, Angus, Shorthorn and Hereford. The maternal effects on weaning weight among the three breeds were significantly different ($P<0.01$). The effects appeared to differ more in two-breed crosses than in backcrosses, but the maternal effect by mating system interaction was not significant. These results are in agreement with Gregory et al. (1965).

In a study of maternal effects on production, Wallace (1964) found that twin-born ewes produced fewer offspring than single-born ewes in a flock which was responding to selection for multiple births. This was possibly due to the lighter weight of twins, which persisted through three years of age in this line. Owen (1957) reported that there was a significant positive correlation between dam's milk production and daughter's fertility at 2 years.

Hohenboken and Brinks (1971a and b) indicated that the most dependable estimates of heritabilities of direct effects and maternal effects on weaning weight were 0.23 to 0.27 and 0.34 to 0.40, respectively. In preweaning growth, slightly more of the variability was associated with maternal effects than with direct effects. However, the most reliable estimate of the genetic correlation of direct and maternal effects was 0.28. This shows that weaning weight of bull calves reflects their own preweaning growth potential and the maternal abilities of their dams.

The results of both investigations by Hohenboken and Brinks (1971a and b) indicated that there is genetic antagonism between additive direct and additive maternal effects on growth. The magnitude of the genetic correlation does not appear large enough, however, to prevent or retard seriously progress from selection for growth.

Brown (1977) reported that estimates of maternal effects were positive with the direct environmental effect contributing the largest fraction of the total phenotypic variance of birth weight, gain from birth to weaning and weaning condition but not in the case of adjusted weaning weight (6.6 percent). In the case of birth weight, percentages were quite high, up to 83.4 percent.

Preweaning growth and weight at 120 and 200 days were studied by Notter et al. (1978b). Animals providing the data were progeny of 564 2-year-old and 569 3-year-old crossbred cows produced by mating Hereford, Angus, South Devon, Simmental, Jersey, Limousin and Charolais bulls to Hereford and Angus cows. They found that 2-year-old animals of all breeds showed positive maternal effects, relative to the Hereford and Angus, on average daily gain and 200 day weight. In 3-year-old animals, ranking for maternal ability matched closely those for milk production. Findings with respect to positive maternal effects on relative growth rate generally agreed with those concerning positive maternal effects on average daily gain. A positive maternal effect on birth weight was sufficient to change the rankings in which 2-year-old Charolais and South Devon crosses and 3-year-old Limousin crosses were included.

Bradford (1972) pointed out that maternal effects may be expected to be more important in sheep than in cattle because of the greater relative variation in litter size in sheep and the fact that many lambs are partially dependent on their mother's milk production until the time of marketing, or at least until they have achieved a higher proportion of their slaughter weight, than is the case with cattle.

A study by Gregory et al. (1978a) was conducted on data from 1207 calves born and 1151 calves weaned in 1973 and 1974 in four breeds, including Brown Swiss, Red Poll, Hereford and Angus, to estimate breed maternal on economic traits of beef cattle. They found that breed maternal effects on calving difficulty were apparent, with the Brown Swiss breed exhibiting the lowest level of calving difficulty. The four breeds differed significantly from each other in breed maternal effects on ADG and 200-day weight, ranking in the order: Brown Swiss, Angus, Red Poll and Hereford. However, the breeds did not differ ($P>0.05$) from each other in breed maternal effects on calf crop weaned. The difference in breed maternal effects was 48.2 kg for 200-day weight between the Brown Swiss and Hereford breeds.

In a study by Gregory et al. (1970b), results showed that in breed maternal effects, the Brown Swiss and Red Poll breeds were superior to the Hereford and Angus breeds in most traits evaluated. For 200-, 400-, and 550-day weight, there were mutual differences averaging 33.4, 31.5 and 27.8 kg ($P<0.01$) respectively, in favor of the females with the Red Poll and Brown Swiss dams in crosses with Hereford and Angus. In

another study (Gregory et al., 1978d) of the Red Poll and Brown Swiss breeds, the breed maternal effects were greatest on carcass traits associated with weight.

In a study of the maternal influence on size in sheep, Hunter (1956) reported that: (1) the maternal organism competes with the foetus for nutrients, thus limiting the size of the young at birth, (2) the maternal influence on the size of young at birth is greater in the larger species which have longer gestation periods than the effect of the genotype of the young and (3) the maternal organism may influence pre-natal foetal growth also by means of some internal secretion or metabolic substance. The influence of the post-natal maternal environment is largely affected through the milk yield of the ewe, and causes of variation in this milk yield were reflected in the post-natal influence. Also, he found that, in lambs at 8 months of age, the lamb's genotype was the most important factor affecting size. The maternal effects on the early-maturing "cannon-bone" length disappeared at 7 months, but at 8 months, 17 percent of the total variation in live weight was still due to the maternal effects. By the time the lambs were about 2 years of age, the effect of the maternal influence would further decrease to a negligible level.

Koch (1972), in a study of maternal effects in beef cattle, found that genetic and permanent environmental components of maternal ability and covariance of individual and maternal effects accounted for 15 to 20 percent of the variation in birth weight and 35 to 45 percent of the variation in daily gain from birth to weaning. In the case of

birth weight, maternal ability of dams did not have a significant direct effect on maternal ability in the next generation.

A study of the relationship between preweaning growth potential and maternal ability pointed out a possible detrimental effect of high growth rate or good maternal environment during the beef heifer's preweaning growth upon her subsequent maternal ability (Christian et al., 1965, and Koch, 1969).

The theoretical composition of correlations of paternal and maternal half-sib correlations, between offspring and dam and between offspring and sire were used to estimate the influence of maternal environment by Koch and Clark (1955a). They suggested that maternal environment from conception to birth and from birth to weaning had a large influence on birth weight, weaning type score and gain from birth to weaning but a small influence on yearling gain and yearling type score.

Analysis of data collected during the period 1926 to 1951 from Hereford calves raised at the U. S. Range Livestock Experiment Station by Koch and Clark (1955b) pointed out that the maternal environment was only slightly significant with respect to yearling gain and yearling type score or was even negatively related to the genes directly influencing these traits. However, maternal environment had a highly significant effect on birth weight, gain from birth to weaning and weaning type score.

In a study of the effect of some genetic and maternal environmental variations in birth weight and gestation length in Holstein cattle, Foote et al. (1959) found that weight and inbreeding of the dam may be considered both as genetic and as maternal environmental variables

working on foetal development. However, weight of dam had a positive effect on birth weight and gestation length.

Koch (1972) reported that maternal environmental effect on gain from birth to weaning appears to be significantly and negatively affected by direct effects of maternal environment from previous generations. He added that the negative relationship between maternal abilities of dam and daughter may be justification for testing alternative rearing systems for male and female calves to obtain consistently high gains. Selecting for improved maternal ability on the basis of weaning gain will be less effective than if there were no direct influence.

Effects of maternal heterosis on postweaning growth and carcass traits of 497 crossbred steers and 356 crossbred heifers produced from 1963 through 1968 were evaluated by Olson et al. (1978). Maternal heterosis effects were unfavorable and largest on first-period growth rate of heifers, but, in steers, these effects were greatest on last-period growth rate. Maternal heterosis effects on carcass traits of steers and heifers at either a constant age or constant weight end point were generally nonsignificant. The unfavorable maternal heterosis for growth rate made for slightly higher fat content of carcasses of progeny of crossbred dams, obviously from the greater milk production of the crossbred cows.

Effects of heterosis of milk production and maternal heterosis on preweaning growth traits were evaluated in reciprocal crossbred and straightbred cows of the Angus, Hereford and Shorthorn breeds by Cundiff et al. The estimate of maternal heterosis was based on the

difference between progeny of crossbred and straightbred dams sired by the same bulls of a third breed. They found that the effect of maternal heterosis on weight at 200 days over all breeds was significantly ($P<0.05$) influenced by age at first calving. The estimates were 3.0 percent ($P<0.01$) vs. 5.8 percent ($P<0.01$) in 2- and 3-year-old first calving management regimes, respectively.

Brown and Galvez (1969) explained that the similarity in composition of sire effect and dam effect differences between paternal and maternal half-sib correlations should be small, and their paternal and maternal half-sib correlations were about the same 0.20 and 0.19, respectively, in Herefords. These results are in agreement with those of Hill (1965) who also found the difference between maternal and paternal half-sib correlations to be small.

A study of maternal influence on body weight in mice by Cox et al. (1959), indicated that postnatal maternal influence was the most important influence on weight through weaning. Most largely controlled by postnatal factors was weight at 12 days. Postnatal maternal influences accounted for 71.5 percent of the variance in 12-day litter weight. The prenatal maternal influences accounted for an additional 9.7 percent of the variance in 12-day litter weight.

A negative genetic correlation between post-natal maternal influence, as measured by 12-day litter weight, and gains from 6 to 8 weeks and a positive genetic relationship between early gain and post-natal maternal influence in mice were found by Young and Legates (1965). These results were similar to those obtained by White et al. (1968).

McDaniel et al. (1969), in a study of the influence of condition on maternal performance of beef cows, from data collected from 3367 Angus, Hereford and Shorthorn calves, found that there was a negative relationship between a heifer's preweaning growth rate and/or condition at weaning and her subsequent performance.

In reporting on studies of some of the factors affecting birth weight, gain from birth to weaning and weaning weight of beef calves, Gregory et al. (1950) stated that the weight of the dam had a significant influence on the birth weight of her offspring. The correlation between weaning weight of the calf and weight of the cow at weaning was not significant and negative in the data from one station (Valentine) but was significant ($P<0.05$) in data from another station (North Platte).

Analysis of data from 214 Hereford cows with 919 calving records, collected during a 12-year period by Hawkins et al. (1965), showed that cows which had the heaviest precalving and early weights on pasture had fewer calves born per cow bred, fewer calves weaned per cow bred and lower adjusted weaning weights. However, cows which weighed less at weaning time weaned more calves and more total pounds of calf. Calf birth weight, weaning type score, weaning condition score, average daily gain from birth to weaning, production testing cow index, parity and year were significant effects on most variables.

III. SIRE EFFECTS

The influences of genetics as measured by sire differences appears to affect production of beef cattle. Most published papers attest to the importance of sire effects on beef cattle traits.

Sire differences ($P<0.05$) in daily gain, were apparent but not in retail yield per day of age as reported by Suess et al. (1966). There were significant differences between sires and among groups in retail yield. Within-herd sire differences were significant in initial weight, initial age, and daily gain.

Analyses of data collected in a crossbreeding experiment conducted by Dearborn et al. (1973) included first-year reproductive performance of 315 daughters of 43 sires and reproductive performance of all heifers and cows mated to 70 bulls. The results indicated that the effect of sires was highly significant ($P<0.01$) on traits that included direct effects of bulls on conception but were not significant ($P>0.05$) in traits that did not include direct effects. This suggests that direct effects influence variation between sires in conception rate more than do transmitted effects.

Using 34 Hereford and 33 Hereford-Red Poll steer and heifer calves, Bradley et al. (1966) indicated that the calves sired by the high-gaining sires had significantly ($P<0.05$) faster preweaning and post-weaning growth rates, less fat thickness and heavier weaning and final weights than did calves sired by low-gaining sires.

Eight Hereford bulls were each exposed during January, February and March of 1966 to 27 to 30 grade Hereford cows by Thrift et al. (1970)

who found sire to be a significant source of variation in weaning weight; cold carcass weight; preweaning average daily gain; estimated boneless, trimmed retail cuts; fat thickness at 12th rib and ribeye area/100 kg carcass. Sire differences in all other traits were small and non-significant. These results are similar to those obtained by Bradley et al. (1966).

Kieffer et al. (1958) found that sire differences were significant with respect to carcass grade, marbling score, slaughter grade and percent bone of the 9-10-11 ribs. Sire differences in fat and lean percentage of the 9-10-11 ribs were small and non-significant. Intra-sire phenotypic correlations of marbling score with tenderness was -0.08, with rate of gain on test, -0.08 and 0.22 with depth of fat over ribeye.

In work reported by Wilson et al. (1967), measurements were recorded from 80 steers and 94 heifers sired by 13 selected polled Hereford bulls over a three-year period. They pointed out that intra-year sire differences were significant ($P<0.01$) in 205-day weight and gain and trimmed loin weight.

Al-Mallah (1975) found sire effects to be highly significant in all traits (Body Weight, Average Daily Gain, Heart Girth, Body Length, Type Score, Condition Score and Hip Width) in both weaning and post-weaning data.

Knapp and Phillips (1942) indicated that some sire apparently produce better post-weaning gain in heifers than in steers while others produce better gaining steers than heifers, suggesting a sire x sex of progeny interaction. They found significant differences between sires in weaning weights, but there was no significant difference between sexes of calves by the same sire.

The influences of sire upon the weaning weights of southwestern range calves were studied using 332 heifer calves and 329 bull calves produced by 11 sires on two ranches during 6 years by Pahnish et al. (1961). Sires had a significant influence on the weaning weight of both heifer ($P<0.01$) and bull calves ($P<0.05$), and bull calves were significantly heavier than heifer calves ($P<0.01$).

Data collected from 80 steers and 94 heifers born between 1963 and 1966 by Wilson et al. (1969) showed that the effects of sires on traits reflecting lean tenderness and the amount and distribution of muscling in absolute units or as ratios to carcass weight were quite pronounced. They found also that sire effects were more important in traits reflecting distribution of muscling in the loin and round than in quality indicators or measurements of waste fat.

IV. HERITABILITY

Dickerson (1947) defined heritability based on total genotypic value in maternally influenced traits as the regression of the sum of the additive genetic values on phenotypic value.

Deese (1967) estimated heritability as the ratio of additive variance to total phenotypic variance. Willham (1963) stated the equation to estimate heritability as follows:

$$h_T^2 = \frac{\hat{\sigma}^2_{An} + 1.5\ \hat{\sigma}^2_{AnAm} + 0.5\ \hat{\sigma}^2_{Am}}{\hat{\sigma}^2_{p}}$$

$\hat{\sigma}^2_{An}$ = additive genetic variance in growth

$\hat{\sigma}^2_{Am}$ = additive genetic variance in maternal effects

$\hat{\sigma}^2_{AnAm}$ = covariance between additive effects on growth

$\hat{\sigma}^2_{p}$ = total phenotypic variance

Butts (1966) reported that in spite of high phenotypic correlations between type and condition at preweaning (approximately 120 days of age), and weaning, type score showed medium heritability (0.40 at weaning) that was higher than that of weaning average daily gain (0.31) and low maternal variance estimates, while condition score had essentially no heritability and a greater response to maternal effects. This is to be expected since fat deposition by the calf can logically be attributed to the milk supplied by the dam, higher milk yield of dams producing fatter calves. When average daily gain was adjusted to remove variation due to differences in condition score the estimate of heritability of adjusted average daily gain was 0.44.

Data analysed by Koch (1972) from 4060 Hereford calves and their parents raised at the Fort Robinson Beef Cattle Research Station, Crawford, Nebraska, yielded estimates of heritability of maternal ability for gain to weaning of 30 to 36 percent. He did not use offspring-dam relationships which may contain a large negative bias. Heritability of maternal ability affecting birth weight was estimated as 25 to 30 percent in Angus and Hereford cattle by Brown and Galvez (1969) while Everett and Magee in (1965) estimated it as 4 to 15 percent in Holsteins.

Heritability of birth weight was estimated to be 0.22 by Everett and Magee (1965). The correlations between the genic maternal ability and the genic ability for birth weight was -0.93 while the heritability of maternal ability of birth weight was 0.04. They concluded that true heritability of birth weight is smaller than estimated heritability of this trait because of negative genetic correlation of birth weight with maternal ability.

Deese (1967) made a study of data collected during the period 1948 to 1963 from two different breeding groups, 725 calves from pure-bred Brahman and 466 calves from a crossbred foundation herd of Brahman-Shorthorn breeding. The calves were from 227 Brahman dams and 208 crossbred dams. He found that the estimate of heritability of maternal and nonmaternal effects on preweaning growth rate were 0.15 and 0.18, respectively, in Brahmans and 0.47 and 0.40, respectively, in crossbreds. The estimates of total heritability of preweaning growth were 0.25 in the Brahmans and 0.17 in the crossbreds.

In a study of maternal and other effects on birthweight of beef calves, Brown and Galvez (1969) pointed out that estimates of heritability of maternal and non-maternal influences on birth weight were 0.30 and 0.56, respectively, in Herefords and 0.25 and 0.14, respectively, in Angus. The estimates of total heritability of birth weight were 0.36 and 0.17 in Hereford and Angus, respectively. Heritability estimates of maternal effects were similar in both sets of data. The estimates of heritability of maternal and non-maternal influences agree with expectations indicated by Koch and Clark (1955a).

Wilson (1973) reported estimates of heritability of hook width and rump length to be quite small (0.12 to 0.18) while those of heritability of heart girth, cannon circumference and length, and body length were moderate to large (0.41 to 0.55) when weight was not held constant. The estimate of heritability of birth weight was 0.39.

For convenient comparison, various published estimates of parameters of interest here are tabulated in Tables 1 and 2.

TABLE 1

ESTIMATES OF HERITABILITY OF VARIOUS TRAITS IN BEEF CATTLE

	Heritability estimates taking maternal environment into account Koch and Clark (1955a)	Heritability estimates Koch and Clark (1955b)	Heritability estimates calculated from the regression of offspring on dam. Koch and Clark (1955c)
Birth weight	0.42	0.35	0.44
Weaning gain	0.12	0.21	0.70
Weaning weight	0.19	0.24	0.11
Weaning type score	0.16	0.18	0.16
Yearling gain	0.40	0.39	0.18
Yearling weight	----	0.47	0.43
Yearling type score	0.27	0.27	0.14

TABLE 2

SUMMARY OF THE RELATIONSHIP BETWEEN CALF GROWTH AND MILK PRODUCTION

Investigator	Results
Knapp and Black (1941)	Correlation of 0.52 between daily gains by calves and milk produced by their dams.
Klett et al. (1965)	Significant ($P < 0.01$) correlations ranging from 0.67 to 0.81 were found when milk yeild was correlated with calf weight at various milking dates in the Angus herd.
Drewry, Brown and Honea (1959)	Calves making largest total gain suckled higher producing cows. Factors other than milk production also may contribute.
Gifford (1953)	Gross correlations were 0.60, 0.71, 0.52, and 0.35 for the first, second, third, and fourth months. Correlations were small and not significant for the last four months of lactation.
Young and Legates (1965)	A positive genetic relationship between early gains and lactation and a negative genetic relationship between later gains and lactation.

CHAPTER III

MATERIALS AND METHODS

I. DATA COLLECTION

Data were obtained at weaning from 1521 Angus calves sired by 145 bulls during a period of ten years (1969 to 1978). Yearling data were obtained from 1388 Angus calves sired by 135 bulls during a period of nine years (1970 to 1978). The calves supplying these data were raised at the University of Tennessee Plateau Experiment Station, Crossville, Tennessee. Number of sires, number of calves, number of bull calves and number of heifer calves in each year are shown in Table 3.

The traits recorded on each animal at weaning (average age 230 days) and at post-weaning (average age 385 days) were:

Average Daily Gain (ADG), unit, lb

Body Weight (BW), unit, lb

Body Length (BL), unit, in

Hip Height (HH), unit, in

Hip Width (HW), unit, in

Fat Thickness (FT), unit, mm

Hide Thickness (HT), unit, mm

Heart Girth (HG), unit, in

Condition Score (CS), subjective score 1 to 16

Type Score (TS), Subjective score 1 to 16

TABLE 3

NUMBER OF SIRES AND CALVES BY YEAR AND SEX (WEANING AND POST-WEANING DATA)

Year	Number of sires		Number of calves		Number of bull calves		Number of heifer calves	
	Weaning	Post-weaning	Weaning	Post-weaning	Weaning	Post-weaning	Weaning	Post-weaning
1969	12	----	134	----	67	----	67	----
1970	15	15	145	147	71	71	74	76
1971	16	15	142	142	79	79	63	63
1972	16	16	155	155	71	71	84	84
1973	14	15	165	156	88	72	77	84
1974	13	14	172	183	95	102	77	81
1975	13	14	196	196	96	97	100	99
1976	16	16	183	193	87	98	96	95
1977	16	16	99	95	55	53	44	42
1978	14	14	130	121	76	71	54	50
	145	135	1521	1388	785	714	736	674

Body measurements are described below.

Body Length (BL) - The distance along the back from the dorsal wither prominence to the posterior prominence of the pin bones.

Hip Height (HH) - The height from ground to the hips.

Hip Width (HW) - The distance between the most prominent lateral projections of the hip bones.

Fat Thickness (FT) - Subcutaneous fat thickness measured ultrasonically on the back between the 12th and 13th ribs about three-fourths of the distance from the dorsal midline to the outer edge of the muscle.

Hide Thickness (HT) - The thickness of the hide measured ultrasonically at the same time as fat thickness.

Heart Girth (HG) - A circumference measurement taken immediately posterior to the shoulders.

Condition Score (CS) - The conventional subjective appraisal of fatness.

Type Score (TS) - A subjective estimate of general conformation.

II. METHOD OF ANALYSIS

All records were adjusted by using constants obtained by least-squares procedures to remove variation due to differences in age of calf, sex of calf and age of dam. Nested within-year analyses were performed on these data by the SAS (1979) Procedures, (Barr et al., 1979) as described in the following models. The first model was used to obtain estimates of components of variance due to sire differences, and the second model

was used to obtain estimates of components of variance due to dam differences. Before the analysis by the second model was conducted, the data were adjusted by least-squares procedures to remove variation due to sire and year differences. It was necessary to use the second model for analyses to obtain estimates of components of variance due to dam differences ($\hat{\sigma}^2_D$) since, had the analyses been conducted on a within-year basis as with the first model, no error mean squares would have been obtained for use in calculating the estimates of $\hat{\sigma}^2_D$. Only a very few cows represented in the data would have had more than one calf in a given year.

(1) $Y_{ijk} = \mu + Y_i + S_j/Y_i + e_{ijk}$

where:

Y_{ijk} = observed value for k^{th} offspring of the j^{th} sire in the i^{th} year

μ = overall mean

Y_i = effect of i^{th} year,

i = 1969, 1970, ---------- 1978. (Weaning)

i = 1970, 1971, ---------- 1978. (Post-weaning)

S_j/Y_i = effect of j^{th} sire within i^{th} year,

j = 1, 2, ---------- 145. (Weaning)

j = 1, 2, ---------- 135. (Post-weaning)

e_{ijk} = random error portion of observation recorded for k^{th} offspring of j^{th} sire in the i^{th} year

(2) $Y_{ij} = \mu + D_i + e_{ij}$

where:

Y_{ij} = observed value for j^{th} calf of i^{th} dam

μ = overall mean

D_i = effect of i^{th} dam, i = 1, 2, --------, 472 (Weaning)

i = 1, 2, --------, 456 (Post-weaning)

e_{ij} = random error portion of observation recorded for j^{th} offspring of i^{th} dam.

These analyses were performed on all data as well as separately on data from bulls and on data from heifers.

Tests of significance were performed using conventional F-tests, even though some question has been raised on theoretical grounds as to absolute appropriateness of error terms in this type of analysis. In spite of the theoretical objection to such tests, researchers routinely perform them on the assumption that negligible error is involved.

The estimate of the component of variance due to differences in maternal influence was calculated as the difference between the estimates of the component of variance due to total variation between dams and the estimate of the component of variance due to sire differences. This is based on the assumption that genic contributions of sire and dam to offspring are equal. Thus, this component of variance would be an estimate of total variance due to differences in maternal influences of dams, both transmitted and environmental influences. Transmitted influences would include effects on offspring of entities transmitted by way of the cytoplasm, of which an ovum contains much more than does a sperm. In the present study, no attempt was made to partition the total

maternal variance into portions due to genic transmission, cytoplasmic transmission and maternal environment.

$$\hat{\sigma}^2_M = \hat{\sigma}^2_D - \hat{\sigma}^2_S$$

where:

$\hat{\sigma}^2_M$ = estimate of variance due to differences in maternal influences of dams

$\hat{\sigma}^2_D$ = estimate of variance due to dam differences

$\hat{\sigma}^2_S$ = estimate of variance due to sire differences

The component of variance due to dam differences is expected to be larger than the component of variance due to sire differences, because the dam influences the offspring by way of transmitted genes, as does the sire, but also by way of the maternal environment she provides and, to a greater extent than does the sire, by way of influences of entities transmitted in the cytoplasm, of which an egg contains much more than does a sperm.

III. FEEDING AND MANAGEMENT

The herd is closed to outside blood, but inbreeding has not yet reached a high level. Yearling bulls were used for one season only and seven-year-old cows were replaced by selected yearling heifers to maintain constant herd size. A limited breeding season was used to cause calving to occur during the winter months of January, February, and March. The cows were grouped approximately July 1 by sex of their calves. Calves nursed until weaning and received no supplemental creep feed.

After weaning calves were kept in dry lot. During the dry-lot feeding period heifer and bull calves received different rations. The heifers were fed corn silage ad libitum, two pounds of hay, two pounds of grain, and a half pound of protein supplement daily. The ration was designed to produce an average daily gain of approximately one pound per day, with limited fat production. The bull calves were daily fed: corn silage, 20 lb; ground whole ear corn (including husks), 5 lb and cottonseed meal, one lb. Both groups received these rations until the beginning of the breeding season the first week of April. The selected yearlings to be added to the breeding herd were then placed on pasture and received no further supplemental feeding until the following winter.

CHAPTER IV

RESULTS AND DISCUSSION

I. NUTRITIONAL EFFECTS

The reason for feeding heifers less than bulls was to afford them with enough nutrients for growth without reducing their future reproductive and milking potential as a result of excessive fat deposition. Maternal influence on avereage daily gain (ADG) to weaning of bulls was higher than that on ADG of heifers, as shown in Appendix Table 10. Genes influencing capacity and gain undoubtedly have an influence also on feed consumed. In the results of Brown et al. (1973b) only hip width did not show a moderate to strong relationship with feed consumed by Angus calves.

II. SIRE EFFECTS

Sire differences in most of the traits at post-weaning were significant ($P<0.01$) except for average daily gain (ADG) and hide thickness (HT), but, at weaning, sire differences were significant ($P<0.01$) in only four traits: average daily gain (ADG), heart girth (HG), condition score (CS), and type score (TS) (Tables 4 and 5). These results agree with those obtained by Al-Mallah (1975).

Differences between sires were responsible for a significant portion of the variance in body weight (BW) of both bull ($P<0.05$) and heifer calves ($P<0.01$), and bull calves were significantly ($P<0.01$) heavier

TABLE 4

ESTIMATES OF VARIANCE COMPONENTS FROM WEANING DATA (SEXES COMBINED)

	$\hat{\sigma}^2_D$		$\hat{\sigma}^2_S$		$\hat{\sigma}^2_M$	
Traits[a]	Estimate	%	Estimate	%	Estimate	%
ADG	0.0548*	72.02	0.0068**	8.78	0.0480	62.40
BW	5457.7400	49.61	213.5810	1.93	5244.1590	47.45
BL	0.6604	12.05	0.0166	1.19	0.6438	11.62
HH	533.3560**	99.31	-1.1829	0.0	-----[a]	----
HW	0.9756*	68.70	0.0226	1.55	0.9530	65.26
HT	0.8697	77.67	0.0033	0.25	0.8663	64.70
FT	6.2420*	90.66	-0.0004	0.0	----	----
HG	8.2620*	63.16	0.4913**	3.72	7.7706	58.90
CS	0.5362	60.69	0.0554**	6.21	0.4808	53.96
TS	0.6158	45.09	0.1604**	11.57	0.4555	32.86

[a]Codes for the traits are defined on page 25.

*$0.01<P<0.05$.

**$P<0.01$.

TABLE 5

ESTIMATES OF VARIANCE COMPONENTS FROM POST-WEANING DATA (SEXES COMBINED)

	$\hat{\sigma}^2_D$		$\hat{\sigma}^2_S$		$\hat{\sigma}^2_M$	
Traits[a]	Estimate	%	Estimate	%	Estimate	%
ADG	0.1268*	63.23	0.0001	0.05	0.1267	62.73
BW	8809.0300**	73.96	280.0140*	2.57	8529.0160	78.15
BL	4.2484**	78.56	0.1204*	2.21	4.1280	75.69
HH	533.0190**	98.83	10.1253**	1.62	522.8937	83.84
HW	0.9586*	67.84	0.0345**	2.37	0.9241	63.46
HT	1.1196	100.00	-0.0028	0.0	-----[a]	-----
FT	6.4101**	92.43	0.0886*	1.18	6.3214	84.10
HG	8.7483*	67.43	0.4940**	3.80	8.2543	63.41
CS	0.9353*	62.68	0.0623**	3.96	0.8730	55.43
TS	0.4940*	49.70	0.0646*	6.47	0.4294	43.00

[a]Codes for the traits are defined on page 25.

* $0.01<P<0.05$.

** $P<0.01$.

than heifer calves. These results are in close agreement with Pahnish et al. (1961). At post-weaning, sire differences in several traits were not significant in either bulls or heifers (Appendix Table 11).

In mammals, it seems logical to expect the importance of maternal influences to become less as the young animal advances in age beyond weaning, especially in traits known to be greatly and directly affected by nutrient supply. However, the changes in maternal variance percentages from weaning to post-weaning shown in Table 6 tend to contradict this a priori notion. Since the maternal variance percentages increased from weaning to post-weaning in most of the traits studied, it appears that cytoplasmic effects are of considerable importance. These effects can continue as direct effects after weaning, whereas, maternal environmental effects cease to be direct effects after weaning.

The ranks of maternal variance percentages shown in Table 7 indicate that the relative responses of the traits to maternal influences change considerably from weaning to post-weaning. There is almost no correlation between the ranks for the same trait at weaning and post-weaning.

III. COMPARISON OF SEPARATE MATERNAL VARIANCE ESTIMATES FROM THE TWO SEXES

The comparisons of changes in maternal variance percentages between weaning and post-weaning in Table 8 show that, in females, as is usually expected the relative importance of maternal influence decreased from weaning to post-weaning in all traits except type score (TS). When

TABLE 6

CHANGES IN MATERNAL VARIANCE PERCENTAGES FROM WEANING TO POST-WEANING (SEXES COMBINED)

Trait[a]	Post-Weaning % - Weaning %
ADG	0
BW	+
BL	+
HH	+
HW	-
HT	-
FT	+
HG	+
CS	+
TS	+

[a]Codes for the traits are defined on page 25.

TABLE 7

RANKS OF MATERNAL VARIANCE PERCENTAGES AT WEANING AND POST-WEANING (SEXES COMBINED)

Traits[a]	Weaning	Post-Weaning
ADG	3	7
BW	6	3
BL	8	4
HH	----[b]	2
HW	1	5
HT	2	----
FT	----	1
HG	4	6
CS	5	8
TS	7	9

[a] Codes for the traits are defined on page 25.

[b] When negative estimates of components of variance were obtained (indicating the parameter to be zero) maternal variance calculations are questionable.

TABLE 8

CHANGES IN MATERNAL VARIANCE PERCENTAGES FROM WEANING TO POST-WEANING BY SEX

Traits[a]	Post-weaning % — Male	Weaning % Female
ADG	-	-
BW	+	-
BL	+	-
HH	+	-
HW	+	-
HT	----[b]	-
FT	-	-
HG	+	-
CS	+	-
TS	+	+

[a]Codes for the traits are defined on page 25.

[b]When negative estimates of components of variance were obtained (indicating the parameter to be zero) maternal variance calculations are questionable.

negative estimates of variance components are obtained, one is hesitant to make definite statements concerning trends from weaning to post-weaning, as in the case of hide thickness (HT).

Apparently, the male data were responsible for the increases in maternal variance percentages from weaning to post-weaning shown in Table 6 (page 36) for the data from both sexes combined since the comparisons shown in Table 8 (page 38) indicate an increase in the maternal variance percentage from weaning to post-weaning in all but two traits in males, average daily gain (ADG) and fat thickness (FT), which showed the expected decrease. These two traits are obviously directly affected by nutrient supply. However, the estimates of maternal variance in fat thickness at both weaning and post-weaning are questionable because of the negative estimates of variance components involved.

Once again, as in the case of estimates from the data from both sexes combined, there are extreme changes in ranks of the traits with respect to maternal variance percentage from weaning to post-weaning in each sex considered separately.

Al-Mallah (1975) found no significant sire x sex interaction which indicates that males and females respond in approximately the same way to differences other than sire differences. That is, sires would rank the same on the basis of male progeny averages and female progeny averages even though females are fed at a restricted level after weaning. Thus, the differences shown in Table 8 (page 38) between males and females with respect to changes in relative importance of maternal influence from weaning to post-weaning indicates that females, during the post-weaning

period, tend to reflect differences in their individual potential for growth more than do males which, apparently, reflect persisting maternal effects during the post-weaning period.

Although somewhat inconsistent, a pattern with respect to relative importance of maternal variance in males and females at weaning and post-weaning can be discerned from Appendix Tables 10 and 11. In general, maternal variance percentages are greater in females at weaning and greater in males at post-weaning. This conforms to the statements made above with respect to the comparisons between the two sexes made in Table 8 (page 38).

A relatively greater maternal variance in males than in females might be construed as circumstantial evidence for sex linkage of genes involved in the heredity of quantitative traits such as those studied here. Perhaps some of the difference between the two sexes at post-weaning as shown in Appendix Table 11 may be attributed to some influence of sex-linked genes since it is known that the exact genetic likeness between dam and son is slightly greater than that between dam and daughter when sex-linked genes are considered.

The results of this study indicate that total maternal variance is of considerable magnitude in several traits both at weaning and post-weaning. However, specific recommendations as to adjustments to remove maternal variance are not justified at this time. Future research should be directed toward obtaining reliable estimates of correlation between traits. The suggestion of Butts (1966), namely, adjusting data on traits of interest in a selection program to remove variance due to differences

in traits which are highly correlated with the traits of interest and which contain large maternal components in their variances, should be considered. After such adjustment, estimates of heritability of the traits of interest would be more reliable, and selection on the basis of adjusted values for the traits of interest would be more effective. Butts (1966) increased the estimate of heritability of average daily gain from 0.31 to 0.44 by adjusting average daily gain to remove variance in it due to differences in condition score, a trait highly correlated with average daily gain and greatly influenced by maternal effects in his study.

The compensatory-gain phenomenon may well be involved in the differences between weaning and post-weaning maternal variances in bulls in this study. Those bulls whose dams provided a high level of nutrition from birth to weaning would tend to gain, on a relative basis, less than those whose dams gave relatively little milk and vice versa.

IV. CONCLUSIONS

1. The heifers tended to follow the expected decline from weaning to post-weaning in importance of maternal effects. However, the bulls did not exhibit this pattern for most of the traits.

2. This research indicates that maternal variance is of considerable magnitude in some traits, increases with age in some traits and decreases with age in others.

3. While there may be some question as to the reliability of the estimates obtained here, there is no obvious reasons to suspect them to be biased.

4. The magnitude of some of the estimates of maternal variance is great enough to warrant further research, for if the total maternal variance is as large as some of the estimates indicate it to be, heritability estimates would be greatly affected by maternal variance.

CHAPTER V

SUMMARY

Data were obtained at weaning from 1521 Angus calves sired by 145 bulls during a period of ten years (1969 to 1978). Yearling data were obtained from 1388 Angus calves sired by 135 bulls during a period of nine years (1970 to 1978). The calves supplying these data were raised at the University of Tennessee Plateau Experiment Station, Crossville, Tennessee. The traits recorded on each animal at weaning (average age, 230 days) and at post-weaning (average age, 385 days) were Average Daily Gain, Body Weight, Body Length, Hip Height, Hip Width, Fat Thickness, Hide Thickness, Heart Girth, Condition Score and Type Score.

Post-weaning feeding was on a relatively high forage, low concentrate ration. Heifers were fed at a restricted level, as compared to bulls to produce an average daily gain of approximately one pound per day, with limited fat production.

All records were adjusted by using constants obtained by least-squares procedures to remove variation due to differences in age of calf, sex of calf and age of dam. Nested within-year analyses were performed. One model was used to obtain estimates of components of variance due to sire differences, and another model was used to obtain estimates of components of variance due to dam differences. Analyses by the second model were performed after adjusting the data to remove variation due sire and year differences. The estimate of the component of variance due to differences in maternal influence was calculated as the difference

between the estimate of the component of variance due to total variation between dams and the estimate of the component of variance due to sire differences.

Results showed maternal influence on average daily gain (ADG) to weaning in bulls to be greater than that on ADG of heifers. Sire differences in all but two traits, average daily gain and hide thickness, were significant ($P<0.01$) at post-weaning, but at weaning, sire differences were significant ($P<0.01$) in only four traits: average daily gain, heart girth, condition score and type score. Differences between sires were responsible for a significant portion of the variance in body weight of both bull ($P<0.01$) and heifer calves ($P<0.01$), and bull calves were significantly ($P<0.01$) heavier than heifer calves. The male data were responsible for the increases in maternal variance percentages from weaning to post-weaning with respect to all but two traits in males, average daily gain and fat thickness which showed the expected decrease. These two traits are obviously directly affected by nutrient supply. The differences between males and females with respect to changes in relative importance of maternal influence from weaning to post-weaning indicate that females, during the post-weaning period, tend to reflect differences in their individual potential for growth more than do males which, apparently, reflect persisting maternal effects during the post-weaning period. In general, maternal variance percentages are greater in females at weaning and greater in males at post-weaning. Maternal variance is of considerable magnitude in several traits both at weaning and post-weaning. However, specific recommendations as to adjustments to remove maternal variance are not justified at this time.

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LITERATURE CITED

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APPENDIX

APPENDIX

TABLE 9

RANKS OF MATERNAL VARIANCE PERCENTAGE AT WEANING AND POST-WEANING BY SEX

Traits[a]	Male		Female	
	Weaning	Post-Weaning	Weaning	Post-Weaning
ADG	1	----	4	----
BW	8	1	2	3
BL	6	5	6	----
HH	----[b]	7	8	----
HW	7	6	5	----
HT	----	----	----	----
FT	4	----	7	2
HG	3	3	1	1
CS	2	2	3	----
TS	5	4	----	4

[a]Codes for the traits are defined on page 25.

[b]When negative estimates of components of variance were obtained (indicating the parameter to be zero) maternal variance calculations are questionable.

TABLE 10

ESTIMATES OF VARIANCE COMPONENTS FROM WEANING DATA (BY SEX)

Traits[a]	$\hat{\sigma}^2_D$				$\hat{\sigma}^2_S$				$\hat{\sigma}^2_M$			
	Male		Female		Male		Female		Male		Female	
	Estimate	%	Estimate	%	Estimate	%	Estimate	%	Estimate	%	Estimate	%
ADG	0.0695**	93.40	0.0365	80.20	0.0080**	11.05	0.0061**	12.75	0.0615	80.69	0.0305	66.23
BW	1359.7600	11.86	10939.6000	93.48	644.1480**	5.79	476.3822*	4.34	715.6120	6.43	10463.2180	95.32
BL	0.9495	18.04	2.9998	56.47	0.3312**	6.09	0.1211	2.15	0.6183	11.36	2.8787	50.95
HH	90.2121**	95.06	10.9690	60.21	-2.2900	0.0	9.9960**	1.60	0.0	0.0	0.9730	0.16
HW	0.1913	15.25	0.9732	75.69	0.0461*	3.29	0.0443	2.87	0.1452	10.31	0.9289	61.20
HT	0.0	0.0	0.0	0.0	0.0932*	7.77	-0.0302	0.0	0.0	0.0	0.0	0.0
FT	2.8351*	85.01	2.7576	84.65	0.1311*	1.69	0.0461	0.63	2.7941	34.91	2.7115	36.68
HG	5.9086	41.37	13.8864	94.47	0.9440**	7.21	0.8420**	6.33	4.9646	37.91	13.0444	98.02
CS	0.5132	76.66	0.8094	76.40	0.0652**	9.56	0.0970**	9.05	0.4480	65.92	0.7124	66.35
TS	0.5313	60.86	-0.6296	0.0	0.1211**	8.79	0.2232**	16.00	0.4102	29.79	0.0	0.0

[a]Codes for the traits are defined on page 25.

*0.01<P<0.05.

**P<0.01.

TABLE 11

ESTIMATES OF VARIANCE COMPONENTS FROM POST-WEANING DATA (BY SEX)

	$\hat{\sigma}^2_D$				$\hat{\sigma}^2_S$				$\hat{\sigma}^2_M$			
	Male		Female		Male		Female		Male		Female	
Traits[a]	Estimate	%	Estimate	%	Estimate	%	Estimate	%	Estimate	%	Estimate	%
ADG	0.2105**	96.51	-0.0432 +	0.0	-0.0051	0.0	0.0062**	6.29 +	0.0	0.0	0.0	0.0
BW	10345.0000**	94.03	1899.8000* +	32.80	279.1690	2.82	83.3170	0.69 —	10065.8310	91.50	1816.4830	15.07
BL	2.3469	44.15	-1.3181 +	0.0	0.1770	3.27	-0.0673	0.0 —	2.1699	40.00	0.0	0.0
HH	15.0482*	82.66	11.6160 +	63.97	2.1690	0.32	13.6070**	2.39 +	12.8792	1.91	-1.9910	0.0
HW	0.4714	36.72	-1.0028 +	0.0	0.0431*	2.93	0.0202	1.36 —	0.4283	29.25	0.0	0.0
HT	0.0	0.0	0.0	0.0	0.0322	2.63	0.0431	3.60 +	0.0	0.0	0.0	0.0
FT	1.1332	34.78	2.1066 —	71.65	-0.0081	0.0	0.1261	1.70 +	0.0	0.0	1.9805	26.63 —
HG	11.1482	75.94	3.9418 +	25.95	0.4230	3.40	0.2440	1.78 —	10.7252	86.17	3.6978	27.06
CS	1.5044	100.00	-0.0330 +	0.0	0.0411*	2.53	0.1432**	9.26 +	1.4633	90.24	0.0	0.0
TS	0.5663	53.11	0.0821 +	8.97	0.0922**	8.47	0.0152	1.61 —	0.4741	43.92	0.0669	7.28

[a]Codes for the traits are defined on page 25.

* $0.01<P<0.05$.

** $P<0.01$.

VITA

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